

PARASITES OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*: FISHERY IMPLICATIONS

R. J. G. LESTER,¹ A. BARNES,² AND G. HABIB³

ABSTRACT

The numbers of 26 types of parasites were counted in 878 fish, of which all but 3 were from 14 areas in the Pacific. Data from the 22 most reliable parasites gave no evidence of discrete stocks of skipjack tuna in the Pacific, either when analyzed singly or when using combinations of parasites in multivariate analyses. New Zealand fish carried many tropical parasites, particularly didymozoids, in numbers similar to fish caught in the tropics, indicating that the bulk of these fish had recently migrated from the tropics. The number of *Tenaculularia coryphaenae*, a larval tapeworm, was positively correlated to fish size in the tropics. In New Zealand, however, fish over 55 cm carried about the same number of *T. coryphaenae* as fish 45 to 55 cm, suggesting they had left the tropics when they were 45 to 55 cm and had not returned.

Analysis of the numbers of parasites from particular schools suggested that school members stayed together for several weeks but not for life.

The use of parasites to delineate stocks for management purposes is a well-established technique. For a comprehensive review of the many examples see MacKenzie (1983).

The skipjack tuna, *Katsuwonus pelamis*, is one of the most valuable fishery resources of the central and western Pacific. At least 50 species of parasites have been reported from it. The distribution of only one, the hemiuroid digenean *Hirudinella ventricosa*, has previously been investigated. In the Atlantic, Watertor (1973) found it in 7% of skipjack tuna off West Africa, 40% off Brazil, and < 1% off Florida. In the Pacific, Nakamura and Yuen (1961) found it in 21% of skipjack tuna off the Marquesas and 34% of fish from Hawaii. Sindermann (1961) pointed out that analyzing the distributions of combinations of parasites may provide more information than the examination of individual species. That, in general, has been our approach here.

In addition, school-school variation in parasite numbers was studied to determine how long schools stayed together, and secondarily to evaluate the degree of permanence of the parasites.

MATERIALS AND METHODS

Of the 878 fish dissected, 386 were collected by the *Hatsutori Maru* on charter to the South Pacific Com-

mission (SPC), 246 by the New Zealand Ministry of Agriculture and Fisheries (NZ), and the remainder by other governments and fishing companies (see Acknowledgments). Fish were obtained from 15 areas (Fig. 1, Table 1).

Gills and viscera were frozen and flown to Brisbane for dissection. The SPC and NZ fisheries officers sampled 5 fish/school from a maximum of 3 schools/d. Commercial companies were unable to sample from individual schools and usually supplied the head and the anterior ventral body, removed from frozen fish by a single slanting cut using a band saw. Fork length, if not supplied, was calculated

TABLE 1.—Sources of fish dissected.

Area	Date	No. fish	Avg. length (cm)
A Palau, Helen R.	Aug. 1980	35	41
B Ponape	July 1980	45	59
C Papua New Guinea	June 1981	30	50
D Papua New Guinea	Nov. 1981	60	41
E Solomon Is.	June 1980	30	46
F Coral Sea	Jan. 1982	19	57
G Fiji	Feb., Mar., Apr., May 1980	100	50
H Norfolk Is.	Mar. 1980	21	57
I New South Wales	Jan. 1981	103	47
J New Zealand, west	Mar. 1980; Jan., Feb. 1982	69	52
K New Zealand, east	Jan. 1980; Jan., Feb. 1982	163	49
L Marquesas	Dec. 1979; Jan. 1980	150	47
M California	Aug. 1981	30	47
N Ecuador	Jan. 1982	20	48
O Atlantic (Puerto Rico)	Mar. 1981	3	50

¹Department of Parasitology, University of Queensland, St. Lucia, Brisbane, Australia 4067.

²Faculty of Science, University of Queensland, St. Lucia, Brisbane, Australia 4067.

³Fisheries Research Division, New Zealand; present address: Southpac Fisheries Consultants, P.O. Box 7230, Auckland 1, New Zealand.

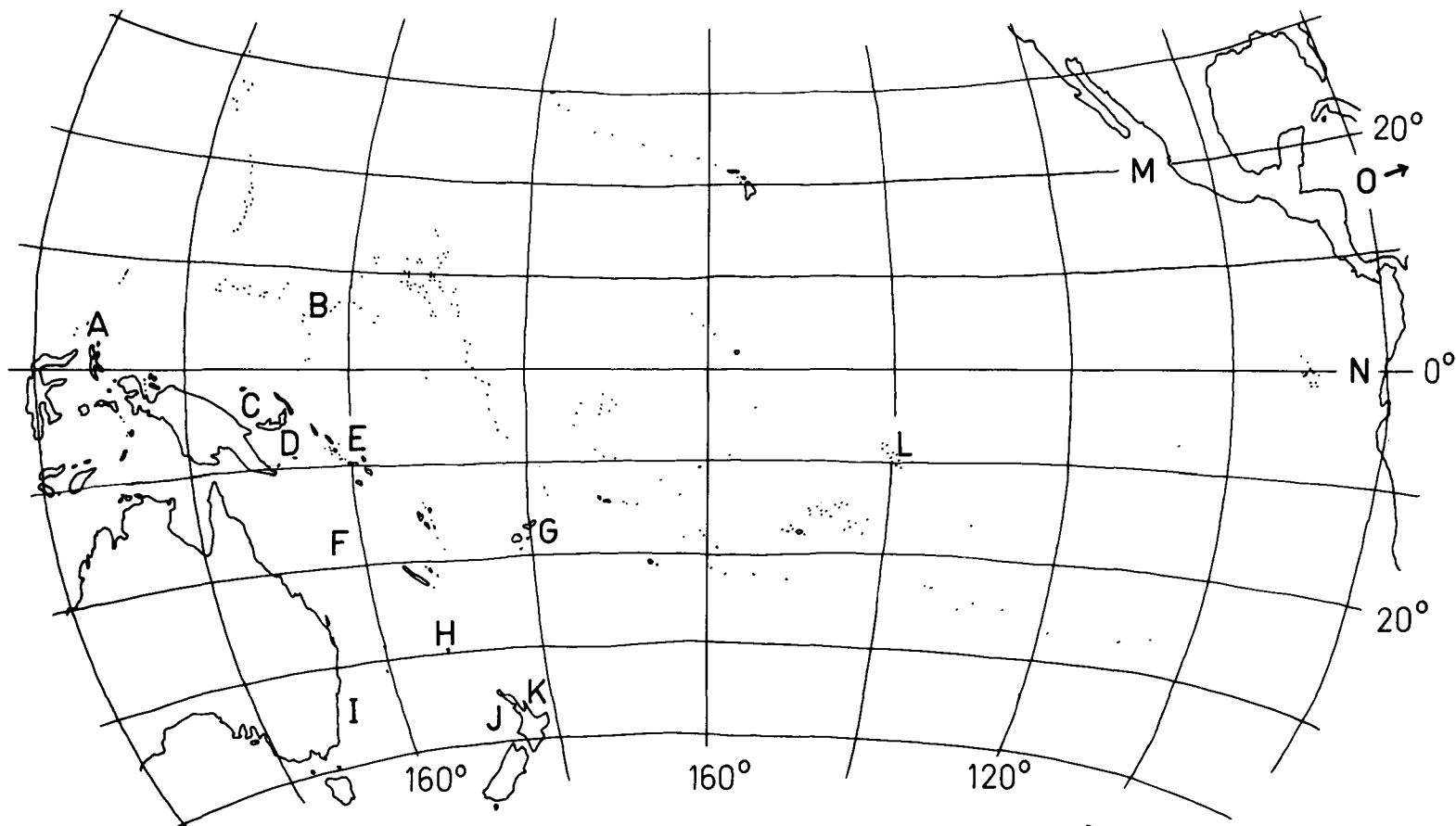


FIGURE 1. - The 15 sites, A to O, from which fish were received for parasitological analysis. A = Palau, Helen Reef; B = Panape; C and D = Papua New Guinea; E = Solomon Islands; F = Coral Sea; G = Fiji; H = Norfolk Island; I = New South Wales; J = New Zealand West; K =

New Zealand East; L = Marquesas Islands; M = California; N = Ecuador; O = Atlantic (Puerto Rico).

from head length using the formula $7.8 + 2.75 \times (\text{head length})$ for heads under 14.5 cm and $-1.7 + 3.3 \times (\text{head length})$ for larger heads (from measurements of 80 and 83 fish, respectively). Prior to dissection, fish were thawed overnight at 6°C. In general, all viscera parasites were counted whereas gill parasites were counted on one side only and the numbers doubled in the final tables. A didymozoid capsule was counted as one parasite though most contained two individuals. Representative parasites were fixed and stored in 10% Formalin⁴ except for nematodes which were fixed and stored in 70% alcohol.

An additional set of data on the abundance of the larval cestode *Tentacularia coryphaenae* was collected at sea by SPC and NZ fisheries officers. They recorded the number of *Tentacularia* visible through the peritoneum in the wall of the body cavity of 1,529 fish.

Besides some summary statistics, two types of statistical analysis were done: 1) investigation into the similarities and dissimilarities of the parasite fauna between the various areas sampled, and 2) a study of school integrity.

The similarities and dissimilarities between areas were examined using a series of cluster analyses and multivariate canonical analyses (Mardia et al. 1979). Strictly speaking, canonical analyses require data which are normally distributed and which have a common variance. However, the frequency distributions of the parasites were not normal. They showed considerable differences from one parasite to

another and most appeared to have two components: one which could be adequately approximated by a negative binomial distribution; and a second component consisting of a disproportionately large zero category, presumably arising because some schools had not been exposed to infection. Precise transformations to normalize the data would thus have been complex and of doubtful accuracy considering the small size of the samples from each school. A single transformation for all species was therefore used: the natural logarithm of the number of parasites plus 1.0.

To avoid possible biases due to associations between parasite numbers and fish length, such as that shown in Figure 2, the transformed counts were then adjusted for fish length. This was done for each species by regressing $\log(\text{parasite number} + 1.0)$ on fish length, for all Pacific tropical fish (489), to estimate the magnitude of any relationship. This was used to adjust the transformed parasite numbers, except where this was zero, to that expected for a fish of a standard length of 50 cm. (This length was very close to the overall mean length of the fish.) The method could not be trusted to eliminate all effects of length, so, as an added safeguard, only fish 39.5 to 57.5 cm were used in the multivariate analyses (83% of the total). These are likely to have been 1 yr old (Uchiyama and Struhsaker 1981; Wankowski 1981).

In a few instances a parasite was absent from all fish in one area. To allow matrix inversion in the canonical variate analyses, a random number between -0.005 and $+0.005$ was added to the data. This did not influence the outcome. The results of the canonical variate analyses were displayed graphically as plots of the first versus the second canonical

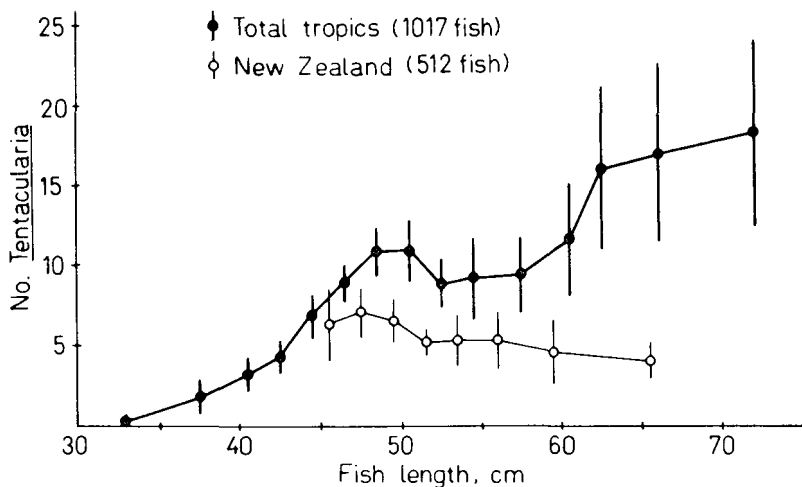


FIGURE 2.—Relationship between number of *T. coryphaenae* and fish length. Mean ± 2 SE. Each mean from minimum of 19 fish. In the tropics the number increased with length but this was not reflected in the New Zealand samples.

⁴Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

axes. Confidence limits (95%) for the positions of different areas on these plots are presented as circles with radius equal to the square root of 5.99/number of fish in sample (Mardia et al. 1979).

Analyses on the same combinations of parasites were also done by calculating minimum spanning trees (Gower and Digby 1981), and dendrograms from nearest neighbor and centroid cluster analyses (Clifford and Stephenson 1975), basing similarity measures on logarithms of area means. Areas were grouped in a similar way by all methods. Using clustering algorithms which either ignored or allowed for matches between areas where parasites were not recorded did not significantly influence results. For these reasons, and because only canonical variate analysis provided some measure of reliability for its conclusions (confidence rings), only the results of the canonical analyses are presented below.

School integrity was examined by comparing the variability in parasite numbers per fish between schools, to that within schools, for the two areas (Marquesas and east New Zealand) where the largest numbers of schools were sampled. This showed which parasites were strongly linked to schools, and also allowed tentative estimation of the length of time schools remained intact. In theory, for parasites to show strong school associations two conditions need to be met: the parasite must heavily infect some schools and not others, and its life span in the fish must be equal to or shorter than the life of the school. Parasites which showed strong school-school association were therefore likely to be shorter lived than those not showing such associations, and other evidence being equal, were considered less reliable as population markers than related species.

Two methods were used to compare within and between school variability in each of the two areas. First, a series of univariate analyses of variance of $\log(\text{parasite numbers} + 1.0)$ were done to calculate the ratio of between school to within school variances. The magnitude of these ratios, and the corresponding probabilities that they do not differ from 1.0, were interpreted as measures of school integrity. A limitation of this method was that the data were only approximately normally distributed, particularly for rare parasites, and thus the derived probabilities were also approximations.

The second method, a median test, was based on the binomial distribution. The number of parasites of a particular species in each fish was transformed to a zero if it was less than or equal to the median number per fish for the area, and to a one otherwise. The zeros and ones of each school were then considered

as a binomial sample. If these samples showed evidence of greater variation than expected by chance (i.e., too many schools with nearly all zeros or nearly all ones), then the schools differed with respect to the distribution of the parasite. A statistic, approximately distributed as a χ^2 random variable, was calculated using GLIM (Baker and Nelder 1978) to determine whether the binomial samples showed evidence of differences. Its associated probability was used as a measure of school integrity. The method had the useful property of being independent of the distribution of parasite numbers. For parasites with a median per fish of <1 , the test was based on the presence or absence of the parasite, though obviously the rarer the parasite the less sensitive the test.

It is possible that some schools were sampled twice. If this did happen, the results of both methods err on the conservative side. Only those species that gave consistent results by both methods were used to draw conclusions about school integrity.

RESULTS

Evaluation of Parasite Species

Information was collected on 26 different types of parasites (species or species complexes) from 15 areas. A summary of the raw data unadjusted for fish length is given in Table 2.

The parasite species were evaluated for their probable longevity on or in skipjack tuna. For them to be useful as markers they needed to be relatively long-lived, preferably surviving for the life of the fish. Nothing was known specifically about their longevity in skipjack tuna, though data were available on related forms (Table 3). In general, intestinal lumen dwellers appear to be more easily lost than larval forms encapsulated in the tissues. The 26 skipjack tuna parasites were divided into four groups, those considered "temporary", "semi-permanent", and "permanent", and those not used at all.

Four parasites were not used in any analyses. Two of the nematodes, *Ctenascarophis* sp. and *Spinitectus* sp. (Nos. 23 and 24 in Table 2), were found in the gut of virtually every fish in which they were sought, from every area. Their small size meant that the number recovered was a function of the time spent searching. They were only counted in every fifth fish, as were the two larval cestodes from the large intestine, *Scolex polymorphus* (large) and *S. polymorphus* (small) (Nos. 25 and 26). Counting these was time consuming, their apparent abundance may have been inversely related to the state of preservation of

TABLE 2.—Average numbers of parasites per fish in all skipjack tuna (878) from the areas listed in Table 1, unadjusted for length. The last column gives the correlation coefficient (r) for length against log (parasite number + 1) for Pacific tropical fish.

No.	Parasites	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	r
1	<i>Caligus</i> spp.	5	17	5	5	10	36	4	3	3	3	1	7	0	1	7	0.37
2	<i>Didymocylindrus filiformis</i>	16	5	2	3	4	4	7	3	6	8	10	4	4	3	10	-0.14
3	<i>Didymocylindrus simplex</i>	16	7	4	6	13	11	14	12	18	26	18	14	15	6	3	-0.08
4	<i>Didymoprolema fusiforme</i>	4	1	0	1	1	1	4	1	4	2	3	3	3	1	1	-0.06
5	<i>Lobatozoum multisacculatum</i>	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.1	0.4	0.2	0.3	0.1	0.0	0.03
6	<i>Syncoelium filiferum</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	13.1	0.0	0.0	0.0	0.0	0.0	0.0	—
7	<i>Philometra</i> sp.	1	3	4	29	5	P ¹	2	2	3	3	1	6	6	1	8	0.02
8	<i>Anisakis</i> type I	1.0	0.2	2.7	1.0	0.7	1.6	0.2	0.5	0.9	2.1	1.5	0.6	0.2	0.1	2.7	0.13
9	<i>Anisakis</i> type II	0.2	0.0	0.0	0.1	0.0	0.1	0.0	0.4	0.1	0.8	0.2	0.0	0.4	1.2	2.3	-0.02
10	<i>Terranova</i> sp.	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.06
11	<i>Coeliodidymocystis</i> sp.	1.3	2.1	0.3	0.2	0.9	0.2	1.2	0.5	0.3	0.7	1.3	0.8	0.1	0.7	0.0	0.03
12	<i>Tentacularia coryphaenae</i>	3	22	P ¹	3	4	19	8	6	4	5	6	10	3	P ¹	P ¹	0.48
13	<i>Oesophagocystis dissimilis</i>	12	6	8	7	8	12	9	3	6	3	9	8	8	9	11	-0.05
14	<i>Kollikeria</i> / <i>Didymocystis</i> spp.	13	4	1	5	9	4	7	7	8	4	5	6	11	5	6	-0.11
15	<i>Dinurus euthynni</i>	55	9	19	35	66	1	2	3	0	0	0	15	0	0	0	-0.34
16	<i>Didymocystoides intestino-muscularis</i> ²	30	27	26	37	49	39	54	18	15	12	16	44	134	17	64	-0.14
17	<i>Hirudinella ventricosa</i>	0.4	0.6	0.4	0.2	1.1	0.7	0.4	0.3	0.1	0.0	0.0	1.1	0.1	0.2	1.0	-0.10
18	<i>Raorhynchus terebra</i>	22	16	13	17	15	18	25	65	4	2	4	12	3	1	0	-0.00
19	<i>Didymocystoides intestino-muscularis</i> ²	14	3	3	9	3	8	5	8	6	6	6	7	13	3	2	-0.24
20	<i>Lagenocystis</i> / <i>Univitellannulocystis</i> spp.	76	40	29	29	22	45	43	16	38	17	30	61	178	34	41	-0.11
21	<i>Tergestia laticollis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.8	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.00
22	<i>Rhipidocotyle</i> sp.	0.0	0.3	0.0	0.2	0.2	2.3	2.4	0.0	1.3	0.0	0.0	0.1	0.0	0.0	0.0	0.08
23	<i>Ctenascaphis</i> type	35	7	6	2	18	22	38	49	7	17	21	33	4	1	108	
24	<i>Spinitectus</i> type	10	7	20	2	12	5	9	10	5	6	18	13	5	3	10	
25	<i>Scolex polymorphus</i> (large)	4	0.4	0.2	0	7	166	33	P ¹	122	101	27	10	161	9	7	
26	<i>Scolex polymorphus</i> (small)	200	124	1,089	287	8,900	257	463	140	211	53	24	206	495	153	105	

¹P = present.²No. 16—stomach; No. 19—intestine.

the fish, and their longevity was doubtful. *Philometra* sp. (No. 7) was found predominantly in developed ovaries, which were present in less than half of the fish sampled. The data were used for comparing school-school variability only.

Seven parasites were considered "temporary". They appeared to be short-lived or easily lost from the fish. The caligid copepods (No. 1, primarily *Caligus productus* in the tropics and *C. bonito* in temperate waters) were not permanently attached and probably moved from fish to fish (Kabata 1981). *Syncoelium filiferum* (No. 6) was common on the gills in New South Wales and New Zealand samples (I, J, and K), but was not recovered from anywhere in the tropics. It is common on fish endemic to New Zealand (D. Blair³). It was considered possibly a temperate short-lived parasite, at least on skipjack tuna, and this was verified by the school integrity study and by conventional tagging data (see later).

Some hemiurids are known to be readily lost from the gut of other species of fish (Table 3). Margolis and Boyce (1969) observed that over half the *Lecithaster gibbosus* were lost from salmon fingerlings

within 3 wk of bringing the fish into captivity. We found *Dinurus euthynni* (No. 15) in all tropical samples from the central and western Pacific but not in the temperate samples I, J, and K. As it showed strong school associations and as the didymozoid data described later showed that New Zealand fish had a recent origin in the tropics, *D. euthynni* was evidently a short-lived tropical parasite that was lost as the fish migrated south. This also appeared to be true for *Hirudinella ventricosa* (No. 17) and possibly for two relatively rare gut-lumen digeneans, *Tergestia laticollis* (No. 21) and *Rhipidocotyle* sp. (No. 22).

In other fish, adult acanthocephalans may be short lived (Table 3). Möller (1976) found that over half the *Echinorhynchus gadi* in three species of fish were lost within 2 wk of the fish being brought into captivity. In our data, *Raorhynchus terebra* (No. 18) was present in reduced numbers in I, J, and K, suggesting it was lost in southern waters. All these parasites then were labelled "temporary".

Didymozoid digeneans were considered "semi-permanent" parasites. In other fish, some didymozoids, or at least the remains of them, are believed to stay in the tissues for the life of the fish. Others, including some species found in the gonads or gills, are lost annually (Table 3). In general, therefore, skip-

³D. Blair, Department of Zoology, University of Canterbury, Christchurch, New Zealand, pers. commun. September 1984.

TABLE 3.—Probable maximum life spans of parasites related to those found in skipjack tuna.

Parasite	Site	Host	Life span	Reference
Acanthocephala				
<i>Echinorhynchus gadi</i>	Intestine	<i>Zoarcetes viviparus</i>	2 wk	Moller (1976)
<i>Echinorhynchus gadi</i>	Intestine	<i>Gadus morhua</i>	6 wk	Moller (1976)
<i>Echinorhynchus gadi</i>	Intestine	<i>Myxocephalus scorpius</i>	7 wk	Moller (1976)
<i>Echinorhynchus gadi</i>	Intestine	<i>Platichthys flesus</i>	11 wk	Moller (1976)
<i>Acanthocephalan</i> sp.	Intestine	<i>Sparus aurata</i>	< 8 wk	Paperna et al. (1977)
Hemiurid Digenea				
<i>Lecithaster gibbosus</i>	Int. and caec.	<i>Oncorhynchus gorboscha</i>	< 9 mo	Boyce (1969)
<i>Lecithaster gibbosus</i>	Int. and caec.	<i>Oncorhynchus gorboscha</i>	> 5 mo	Margolis and Boyce (1969)
<i>Lecithaster gibbosus</i>	Int. and caec.	<i>O. keta</i>	8 mo	Margolis and Boyce (1969)
<i>Tubulovesicula lindbergi</i>	Stomach	<i>O. keta</i>	> 31 mo	Margolis and Boyce (1969)
<i>Lecithophyllum botryophorum</i>	Stomach	<i>Argentina silus</i>	10 mo	Scott (1969)
Didymozoid Digenea				
<i>Nematobothrium texomense</i>	Ovary	<i>Ictiobus bubalus</i>	> 8 mo	Self et al. (1963)
<i>Neometadidymozoon heliciis</i>	Buc. cav.	<i>Platycephalus fuscus</i>	1 yr	Lester (1980)
<i>Nematobothrium spinneri</i> (eggs)	Muscle	<i>Acanthocybium solandri</i>	> host	Lester (1980)
Larval Cestoda				
<i>Gilquinia erinaceus</i>	Mesentery	<i>Melanogrammus aeglefinus</i>	> host	Lubieniecki (1976)
Trypanorhynch sp.	Mesentery	<i>Clupea harengus</i>	> 1 yr	Sindermann (1961)
<i>Triaenophorus crassus</i>	Mesentery	<i>Oncorhynchus</i> spp.	> host	Margolis (1965)
Larval Anisakinae				
Larval anisakid	Mesentery	<i>Clupea harengus</i>	> 1 yr	Sindermann (1961)
Larval anisakid	Mesentery	marine fish	several years	Margolis (1970)
<i>Porrocaecum decipiens</i>	Mesentery	<i>Gadus morhua</i>	several years	Platt (1976)

jack tuna didymozoids were thought to be in the fish probably for at least several months. However, there was some suggestion that 3 of the 10 skipjack tuna didymozoids had a shorter adult life span than the others. Didymozoid No. 16 was much less common in New Zealand waters than in the tropics (Table 4), and didymozoid Nos. 19 and 20 were also less common and, in addition, showed strong school associations (see later). These three didymozoids (possibly representing four species) were omitted from the analysis for Figure 3.

The remaining four parasites (Nos. 8, 9, 10, and 12) were classed as "permanent". Larval cestodes and nematodes, particularly those found in the tissues, are generally believed to survive for several years, often for the life of the fish (Table 3). They

have been used successfully many times as fish population markers (see MacKenzie 1983). In skipjack tuna, the larva of a trypanorhynch cestode, *Tentacularella coryphaenae*, was found in the wall of the body cavity and occasionally in the viscera. No degenerating forms were seen, suggesting that it survived for an extended period and hence could be an excellent population marker, though counts were not available from areas C, N, and O. Larval anisakids were found on the wall of the stomach or in the mesentery. The literature suggested that they should also be good long-term markers (Table 3). They were counted in all areas.

Protozoan parasites have been used successfully to separate stocks of several species of fish. However, none has been reported from skipjack tuna, and we found none in this study.

Relationships Between Areas

Analyses of individual distributions of permanent and semipermanent parasites showed that the abundances of individual parasites varied across the Pacific. However, these differences were inconsistent, the pattern established by one parasite being in conflict with that of a second, and so on.

The data from the three anisakid nematodes and the seven didymozoids considered longest lived were therefore analyzed using canonical variate analysis. Because of the more permanent nature of these parasites and the completeness with which they were recorded from all areas, these data were considered the most reliable for statistically assessing the similarities and dissimilarities between areas. The first three canonical axes accounted for 75% of the

TABLE 4.—Average number of didymozoids in New Zealand fish (all lengths) compared with fish caught in the tropical western Pacific (areas A, B, C, D, E, F, G, and L). In parentheses, $\log(x + 1)$ length-adjusted means for fish 40 to 57 cm only.

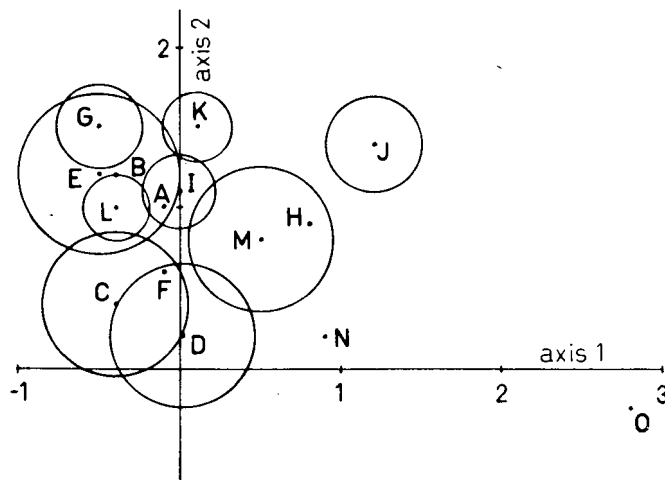
No. ¹	Parasite	New Zealand	Tropics
2	<i>D. filiformis</i>	9 (1.1)	6 (0.8)
3	<i>D. simplex</i>	20 (1.7)	12 (1.3)
4	<i>D. fusiforme</i>	2.7 (0.6)	2.5 (0.5)
5	<i>L. multisacculatum</i>	0.3 (0.1)	0.1 (0.0)
11	<i>Coeliodidymocystis</i> sp.	1.1 (0.4)	0.9 (0.3)
13	<i>O. dissimilis</i>	7 (1.3)	9 (1.9)
14	<i>Kollikeria</i> / <i>Didymocystis</i> spp.	5 (1.2)	6 (1.5)
16	<i>D. intestinomuscularis</i> ²	15 (1.8)	41 (3.3)
19	<i>D. intestinomuscularis</i> ³	6 (1.3)	7 (1.4)
20	<i>L. katsuoni</i> / <i>U. katsuoni</i>	26 (1.9)	47 (2.3)
	No. of fish	232 (213)	469 (364)

¹Code no. from Table 2.

²Stomach.

³Intestine.

FIGURE 3.—Results of multivariate analysis using 3 "permanent" and 7 "semipermanent" parasites (Nos. 2, 3, 5, 8, 9, 10, 11, 13, and 14). Values for first two canonical vectors plotted, and 95% confidence rings indicated for samples of more than 24 fish. The letters refer to the sampling sites indicated in Figure 1.



variation in area-to-area differences in parasite numbers. A plot of the first two, accounting for 58% of the variation, showed the Atlantic fish (O) to be distinct from all the Pacific ones, even though only three fish from the Atlantic were dissected (Fig. 3). However, fish from California (M) and Ecuador (N) fell close to the western Pacific samples. They were separated out on the third axis (not shown), but nevertheless it is evident that they had a somewhat similar parasite fauna. The fish from western New Zealand (J) appeared distinct, and so too, to a less extent, were the Papua New Guinea samples (C and D). There is no suggestion that fish from Ponape (A), Palau (B), Solomon Islands (E), Fiji (G), and the Marquesas (L) had distinct faunas of these long-lived parasites.

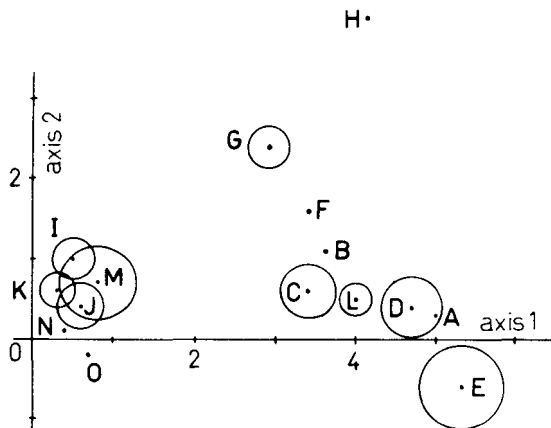


FIGURE 4.—Results of multivariate analyses using 7 “temporary” parasites (Nos. 1, 6, 15, 17, 18, 21, and 22). 95% confidence rings given for samples of more than 24 fish.

In this analysis, *Anisakis* II had the most powerful discriminating properties, though at least 7 of the 10 parasites used were capable of substantial discrimination in their own right.

An analysis based on the 7 “temporary” parasites (Nos. 1, 6, 15, 17, 18, 21, and 22) produced a much greater separation of areas (Fig. 4). They are grouped into two broad classes: one containing New South Wales (I), New Zealand (J, K), and the eastern New Pacific (M, N); and the other the western tropical areas. Each area in the latter group had a temporary parasite fauna that was distinct from most other areas. Over 83% of the variation was accounted for by the first two axes, and 90% by the first three. It is interesting to note that New South Wales (I) is more similar to east New Zealand (K) than to west New Zealand (J) (this was much more marked on the third axis, not shown, where I and K were pulled to one side), and that west New Zealand is similar to California (M) and Ecuador (N).

Taken together, Figures 3 and 4 indicate that several distinct skipjack tuna parasite faunas existed within the tropical Pacific, and the longer lived parasites were more evenly distributed than the shorter lived ones.

To check these results and to look for links between the New Zealand fish and the tropical areas, the west Pacific data were reanalyzed using first the 10 “semipermanent” parasites (the didymozoids) and second the 4 “permanent” parasites (anisakids and *T. coryphaenae*).

The average numbers of didymozoids in the New Zealand fish were almost identical to the overall average for the central and western tropics (Table 4). In the multivariate analyses, the temperate water samples fell to one side of the tropical samples (Fig. 5

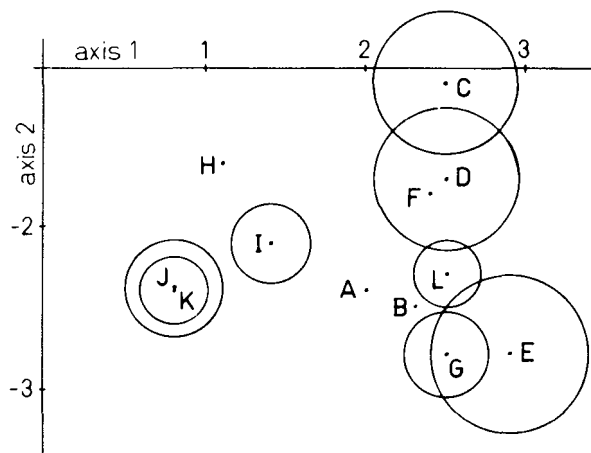


FIGURE 5.—Results of multivariate analysis using 10 didymozoids only (Nos. 2, 3, 4, 5, 11, 13, 14, 16, 19, and 20). 95% confidence rings given for samples of more than 24 fish.

–H, I, J, K), possibly because of the three didymozoids suspected of being relatively short-lived (Nos. 16, 19, and 20). The east and west New Zealand samples (J, K) were identical on the first two axes, and separated only slightly on the third axis (not shown). There was no obvious link between New Zealand and any particular tropical area.

Similarly, the larval nematodes and *T. coryphaenae* (Nos. 8, 9, 10, and 12) did not suggest a link between New Zealand fish and those from any particular tropical area (Fig. 6). However, west New Zealand (J) now appeared distinct from east New Zealand (K) and New South Wales (I). The separation was due to areas having either high *Anisakis* I and II and low *Terranova* and *T. coryphaenae* or low *Anisakis* I and II and high *Terranova* and *T. coryphaenae*. West New Zealand (J) was at one extreme (high *Anisakis*) and the three most northwestern areas—Ponape (B), Fiji (G), and Marquesas (L)—at the other. *Tentacularia coryphaenae* and probably *Terranova* were picked up in the tropics. It seems likely that one or both of the *Anisakis* larvae were picked up predominantly in temperate waters, particularly in west New Zealand. This may explain the separation of west New Zealand from the other areas in Figure 4.

In summary, the New Zealand fish were not closely aligned with any particular tropical sample, and the eastern and western New Zealand fish were probably carrying similar parasite faunas when they arrived in New Zealand.

Tentacularia coryphaenae

Data on this parasite are presented in detail because we had more than for any other parasite and because potentially it was our most valuable marker. It also was the subject of many queries from skipjack tuna processors. The parasite was common throughout the south, central, and west Pacific (Table 3, parasite No. 12). The means of samples of over 22 fish within the length range 44 to 53.9 cm suggested an east-west cline across the Pacific, with twice as many parasites being found in fish from around the Marquesas (L) as around Papua New Guinea (C and D) (Fig. 7). A regression analysis of number of parasites against longitude using tropical data on the number of parasites in 972 fish, transformed and adjusted for differences in host length (data collected independently by the SPC), showed that the relationship was statistically significant, though it only accounted for about 7% of the fish-to-fish variation.

Considering fish of all sizes, the number of *T. coryphaenae* in the tropics increased with the size of the

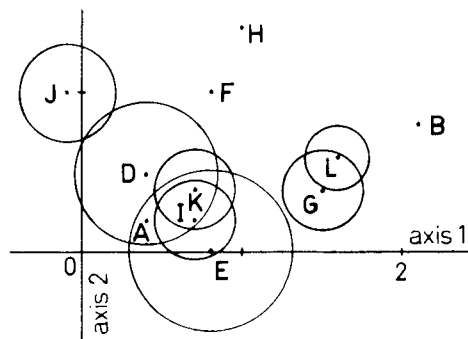


FIGURE 6. – Results of multivariate analysis using the four “permanent” parasites (anisakids and *T. coryphaenae*, Nos. 8, 9, 10, and 12). 95% confidence rings given for samples of more than 24 fish.

fish (Fig. 2, solid circles). The increase around 47 cm is due to many of the Marquesas fish being this size and Marquesas fish tended to have more *T. coryphaenae*. In New Zealand, smaller fish had about the same average number as fish from the tropics. However, this number did not increase with size (Fig. 2, open circles). Thus, the 58+ New Zealand fish had fewer parasites than their peers in the tropics, and about the same number as the 45 to 50 cm fish.

School-to-School Variation

An analysis of variance, and a median test, were carried out on 30 schools from the Marquesas and 19 schools from eastern New Zealand (areas L and K, respectively, Table 5). The results of the two methods on each data set show close agreement.

In the Marquesas, five parasites showed strong evidence of association with particular schools, i.e., the probability that schools differed was at least 0.95 with both methods. The parasites were *Caligus* spp. (No. 1), *D. euthynni* (No. 15), *H. ventricosa* (No. 17), *D. intestinomuscularis* (No. 19), and *Lagenocystis/Univitellannulocystis* spp. (No. 20). For these parasites to show significant differences, they must have heavily infected some schools and not others, and their life span in the fish must have been equal to or shorter than the life of the school. The literature review suggested that the first three species could possibly be readily lost from fish, and this is vindicated by their strong school association. The evident impermanence of the last two, however, was unexpected. It was as a consequence of this finding that they were not included in the analysis for Figure 3.

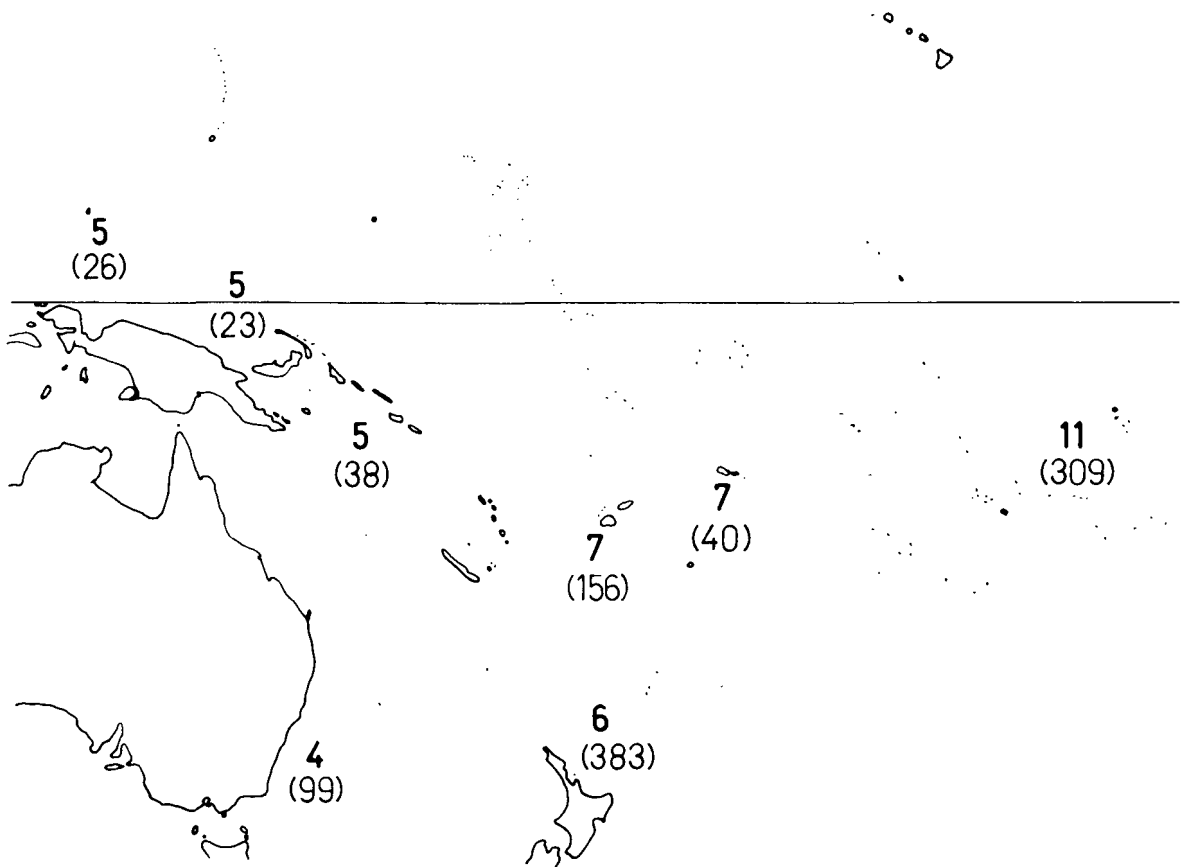


FIGURE 7. — The average numbers of *T. coryphaenae* in skipjack tuna 44 to 53.9 cm long in samples of over 22 fish. Note that the number increased to the east. (In parentheses, number of fish sampled.)

Several other parasites thought to be short-lived, such as *R. terebra*, did not show up in the test, presumably because their infective stages were relatively evenly distributed in the tropical Pacific.

In New Zealand, parasites showing close association with particular schools (using both tests) were *L. multisacculatum* (No. 5), *S. filiferum* (No. 6), *Philometra* sp. (No. 7), *Coeliodidymocystis* (No. 11), *T. coryphaenae* (No. 12), *R. terebra* (No. 18), and *D. intestinomuscularis* (No. 19). *Syncoelium filiferum* and *R. terebra* were both thought to be temporary parasites that could be gained in New Zealand or adjacent waters (Norfolk Island). The origin of the *Philometra* was unknown. Their number reflected the state of maturity of the fish and this varied between schools. However, we were left with three didymozoids and *T. coryphaenae*, all of which differed markedly between schools in eastern New

Zealand. One of the didymozoids, *L. multisacculatum*, a normally rare tropical parasite, was found on all five fish from one school (numbers per fish 1, 2, 8, 3, and 1). As the three didymozoids and *T. coryphaenae* are essentially tropical parasites, the schools had evidently not fully mixed while in temperate waters.

If this is true, these four parasites could not have been picked up uniformly across the Pacific. Evidence is given above that *D. intestinomuscularis* (No. 19) was not picked up uniformly even within the Marquesas. For the other species, a comparison of their mean numbers per fish per school in different areas of the tropical Pacific showed that *Coeliodidymocystis* sp. and particularly *T. coryphaenae* were indeed more abundant in some areas than others. *Lobatozoum multisacculatum* was too rare for any conclusions to be drawn in this respect.

TABLE 5.—Comparison of within and between school variability in numbers of parasites per fish for two areas.

Parasite no. (see Table 3)	Marquesas		New Zealand	
	Analysis of variance ¹	Median test ²	Analysis of variance	Median test
1	***	***		
2		**		
3		*		
4				
5			***	**
6	(no parasites found)		***	***
7			*	*
8		*		
9				
10			(no parasites found)	
11			*	*
12			*	***
13				*
14				
15	***	**	(no parasites found)	
16				
17	*	*		
18			***	***
19	***	***	*	***
20	**	***		
21	*			
22				

¹The probabilities that the ratio of the between and within school variances is no greater than one. (Based on transformed data, i.e., log (parasite no. + 1.0).)

²The probabilities that the proportion of fish with more than the area median is the same for all schools.

*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; blank = $P > 0.05$.

Rate of Mixing of Schools

To estimate the rate of mixing of schools we needed to know the distribution of the parasites among schools before, and after, some known time interval. This we did not have for any of the Marquesas samples.

In New Zealand, however, some approximate calculations could be made because schools arrived from the tropics at different times. Sixteen of the 19 east New Zealand schools were of similar-sized fish and were all caught within 1 mo. These schools were divided into two groups: "early arrivals" and "recent arrivals". (This was done by ranking the schools using a combination of four parasites whose prevalences were positively correlated with each other, Nos. 16, 18, 19, and 20, and which were thought to be relatively short-lived parasites picked up in the tropics. Thus high numbers indicated a recently arrived school.) From catch data (Habib et al. 1980), we calculated that there was an average of 3 to 4 wk between the capture of 25% and 75% of the annual catch. This interval was taken as the approximate period between the arrival times of the early group and the recent group. If mixing was occurring, one would expect that the school-school

differences for tropical parasites would be greater when the fish first arrived (the recent arrivals) than after they had been there for a few weeks (the early arrivals). However, this we could not demonstrate. Our sample sizes at this point were rather small (eight schools in each category), and in fact the reverse appeared to be the case, the early schools having a generally higher variability than the recent arrivals. This suggested that the early arrivals had come from several areas (and still had not fully mixed), whereas many of the later arrivals had perhaps come from one area.

DISCUSSION

Ten of the 26 parasites counted were species of didymozoid trematodes. These are almost exclusively a tropical group. Yamaguti (1970), for example, found 84 different species of didymozoid in fish around Hawaii. None were recorded in checklists of parasites from New Zealand (Hewitt and Hine 1972) or Canada (Margolis and Arthur 1979). Thus, although skipjack tuna are caught in both tropical and temperate waters, their didymozoid infections are evidently picked up primarily in the tropics.

Larval didymozoids have been found in small fish and in invertebrates. It is almost certain that the definitive host becomes infected by feeding on an infected intermediate host (Cable and Nahhas 1962; Nikolaeva 1965). In the tropics skipjack 40 to 60 cm in length feed largely on fish, squid, and stomatopods (Argue et al. 1983). In New Zealand, however, they feed almost exclusively on euphausiids (Habib et al. 1980, 1981). This completely different diet in New Zealand, together with the fact that no endemic New Zealand fish are known to carry any didymozoids, lead us to the conclusion that few, if any, didymozoids are picked up in New Zealand waters.

The occurrence of 10 species of didymozoids in skipjack tuna caught in New Zealand, in numbers very similar to fish of the same size caught in the tropics, thus indicates that New Zealand and tropical fish were found until recently in a similar tropical environment. Almost certainly, the New Zealand fishery is based on fish that have recently migrated from the tropics, and not on fish recruited as post-larvae in temperate waters. This disagrees with tagging data which show that the bulk of New Zealand skipjack tuna of known origin were off New South Wales 10 mo earlier. However, the tagging inference is applicable to < 4% of the total New Zealand fish (Argue and Kearney 1983). Our conclusion is in agreement with Argue et al. (1983) who found no juvenile skipjack tuna in the stomachs of adults from

subtropical waters, though juveniles formed a significant component of the adult diet in the tropics.

The absence of degenerating *T. coryphaenae* and the positive correlation of parasite number and host length suggest that the parasite was long-lived and accumulated in the fish with age. The low numbers of *Tentacularia* in the 57+ cm fish caught in New Zealand indicate that these fish have had a different history from their peers in the tropics. The bulk of the skipjack tuna caught in New Zealand are 45 to 55 cm long. Less than 10% measure 60 cm or more (Habib et al. 1980, 1981). We have concluded above that the majority of New Zealand fish recently arrived from the tropics. The *T. coryphaenae* data indicate that the 57+ cm fish left the tropics at 45 to 55 cm long and have not returned. Evidently as fish age, they become less migratory. This was hypothesized by Kearney (1978).

Large fish were not necessarily permanent residents in New Zealand, however. Of 17 57+ cm fish on which full dissections were carried out, 2 were carrying the acanthocephalan *R. terebra*, a parasite thought to be relatively short-lived (see above) and not picked up in New Zealand. *Raorchynchus terebra* was common in fish from Norfolk Island (area H). Thus some of the large fish may have recently come from areas as far away as Norfolk Island.

The first two canonical variate analyses comparing all areas sampled suggested that fish 40 to 57 cm long had moved between areas and carried the longer lived parasites with them. Parasitologically, there was no evidence of more than one stock of skipjack tuna in the Pacific. Richardson (1983) observed an east-west cline in the gene frequency of two enzymes across the Pacific. From an analysis of 200 gene frequencies he proposed an "isolation by distance" model for skipjack tuna. In this, the degree of mixing of skipjack tuna genes was inversely proportional to the distance between the spawning areas. Tagging data have confirmed that there is some mixing of adult skipjack tuna in the central and western Pacific (Kleiber and Kearney 1983), though more than 95% of the tagged fish recovered during the SPC program were caught within 1,000 mi of their point of release (Kearney 1982).

Schools of skipjack tuna have been observed to break up when feeding (Forsberg 1980). This and observations from aircraft where schools have been seen to merge and later separate (Habib unpubl. obs.) have led to the hypothesis that skipjack tuna do not remain in a particular school for more than a day or so. Certainly the pattern of recovery of SPC tags suggested that tagged skipjack tuna underwent considerable mixing amongst schools soon after release

(Argue and Kearney 1983). However, using Marquesas data we found that several parasites showed strong school associations, particularly didymozoid Nos. 19 and 20 (*D. intestinomuscularis* and *Lagenocystis/Univitellanulocystis* spp.). In another didymozoid, *Neometadidymozoon helici* from the gills of *Platycephalus fuscus*, it takes up to a year for the worms to migrate through the tissues, pair up, mature, and die (Lester 1980). Though only a short migration is needed for didymozoids 19 and 20, as they are intestinal parasites, the worms are still likely to be in the skipjack tuna for a period of weeks. Thus, their strong association with particular schools suggests that school half-life is likely to be in terms of at least weeks rather than days.

In New Zealand, the large school-school differences observed in the numbers of *T. coryphaenae* and several other tropical parasites, especially in the early arrivals, indicate that at the time of catching, the New Zealand schools had not mixed sufficiently to mask their previously distinct tropical faunas.

Do schools remain intact for an extended period, perhaps for the life of the fish? Sharp (1978) found evidence of genetic similarity between individuals in core schools, suggesting that some members of the school were siblings. However, none of *L. multisacculatum*, *Coeliodidymocystis* sp., or *T. coryphaenae*, three long-lived parasites that showed significant school-school differences in New Zealand, showed any significant differences in the Marquesas. This suggests that within the probable long life of these parasites, fish caught in the Marquesas had changed schools and had thus obscured any patchiness in the distribution of the infective stages of the parasites. The parasitological data, then, do not support the hypothesis that fish stay in the same school for life.

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LITERATURE CITED

- ARGUE, A. W., F. CONAND, AND D. WHYMAN.
1983. Spatial and temporal distributions of juvenile tunas from stomachs of tunas caught by pole-and-line gear in the central and western Pacific Ocean. Tuna Billfish Assess. Programme Tech. Rep. 9, 47 p. South Pacific Commission, Noumea, New Caledonia.
- ARGUE, A. W., AND R. E. KEARNEY.
1983. An assessment of the skipjack and baitfish resources of New Zealand. Skipjack Survey Assess. Programme Final Ctry. Rep. 6, 68 p. South Pacific Commission, Noumea, New Caledonia.
- BAKER, R. J., AND J. A. NELDER.
1978. Generalised linear interactive modelling. Numerical Algorithms Group, Oxford, Engl., 184 p.
- BOYCE, N. P.
1969. Parasite fauna of pink salmon (*Oncorhynchus gorbuscha*) of the Bella Coola River, central British Columbia, during their early sea life. J. Fish. Res. Board Can. 26:813-820.
- CABLE, R. M., AND F. M. NAHHAS.
1962. *Lepus* sp., second intermediate host of a didymozoid trematode. J. Parasitol. 48:34.
- CLIFFORD, H. T., AND W. STEPHENSON.
1975. An introduction to numerical classification. Acad. Press, N.Y., 229 p.
- FORSBERG, E. D.
1980. Synopsis of biological data on the skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758), in the Pacific Ocean. IATTC Spec. Rep. 2, p. 296-360.
- GOWER, J. C., AND P. G. N. DIGBY.
1981. Expressing complex relationships in two dimensions. In V. Barnett (editor), Interpreting multivariate data, p. 83-118. Wiley, N.Y.
- HABIB, G. I. T. CLEMENT, AND K. A. FISHER.
1980. The 1979-80 purse-seine skipjack fishery in New Zealand waters. N.Z. Fish. Res. Div. Occas. Publ. 29:1-43.
1981. The 1980-81 purse-seine skipjack fishery in New Zealand waters. N.Z. Fish. Res. Div. Occas. Publ. 36:1-52.
- HEWITT, G. C., AND P. M. HINE.
1972. Checklist of parasites of New Zealand fishes and of their hosts. N.Z. J. Mar. Freshw. Res. 6:69-114.
- KABATA, Z.
1981. Copepoda (Crustacea) parasitic on fishes: problems and perspectives. Adv. Parasitol. 19:1-71.
- KEARNEY, R. E.
1978. Some hypotheses on skipjack (*Katsuwonus pelamis*) in the Pacific Ocean. South Pac. Comm. Occas. Pap. 7, 23 p. South Pacific Commission, Noumea, New Caledonia.
1982. An assessment of the skipjack and baitfish resources of Fiji. Skipjack Survey Assess. Programme Final Ctry. Rep. 1, 48 p. South Pacific Commission, Noumea, New Caledonia.
- KLEIBER, P., AND R. E. KEARNEY.
1983. An assessment of the skipjack and baitfish resources of Kiribati. Skipjack Survey Assess. Programme Final Ctry. Rep. 5, 49 p. South Pacific Commission, Noumea, New Caledonia.
- LESTER, R. J. G.
1980. Host-parasite relations in some didymozoid trematodes. J. Parasitol. 66:527-531.
- LUBIENIECKI, B.
1976. Aspects of the biology of the plerocercoid of *Grillotia erinaceus* (van Beneden, 1858) (Cestoda: Trypanorhyncha) in haddock *Melanogrammus aeglefinus* (L.). J. Fish. Biol. 8: 431-439.
- MACKENZIE, K.
1983. Parasites as biological tags in fish population studies. Adv. Appl. Biol. 7:251-331.
- MARDIA, K. V., J. T. KENT, AND J. M. BIBBY.
1979. Multivariate analysis. Acad. Press, N.Y., 521 p.
- MARGOLIS, L.
1965. Parasites as an auxiliary source of information about the biology of Pacific salmon (Genus *Oncorhynchus*). J. Fish. Res. Board Can. 22:1387-1395.
1970. Nematode diseases of marine fishes. In S. F. Snieszko (editor), A symposium on diseases of fishes and shellfishes, p. 190-208. Am. Fish. Soc. Spec. Publ. 5.
- MARGOLIS, L., AND J. R. ARTHUR.
1979. Synopsis of the parasites of fishes of Canada. Bull. Fish. Res. Board Can. 199, 269 p.
- MARGOLIS, L., AND N. P. BOYCE.
1969. Life span, maturation, and growth of two hemiurid trematodes, *Tubulovesicula lindbergi* and *Lecithaster gibbosus*, in Pacific salmon (genus *Oncorhynchus*). J. Fish. Res. Board Can. 26:893-907.
- MÖLLER, H.
1976. Reduction of the intestinal parasite fauna of marine fishes in captivity. J. Mar. Biol. Assoc. U.K. 56:781-785.
- NAKAMURA, E. L., AND H. S. H. YUEN.
1961. Incidence of the giant trematode, *Hirudinella marina* Garcin, in skipjack tuna, *Euthynnus pelamis* (Linnaeus), from Marquesan and Hawaiian waters. Trans. Am. Fish. Soc. 90: 419-423.
- NIKOLAEVA, V. M.
1965. On the developmental cycle of trematodes belonging to the family Didymozoidae. [In Russ.] Zool. Zh. 44:1317-1327.
- PAPERNA, I., A. COLONNI, H. GORDIN, AND G. W. KISSIL.
1977. Diseases of *Sparus aurata* in marine culture at Elat. Aquaculture 10:195-213.
- PLATT, N. E.
1976. Codworm - a possible biological indicator of the degree of mixing of Greenland and Iceland cod stocks. J. Cons. Perm. Int. Explor. Mer 37:41-45.
- RICHARDSON, B. J.
1983. Distribution of protein variation in skipjack tuna (*Katsuwonus pelamis*) from the central and south-western Pacific. Aust. J. Mar. Freshw. Res. 34:231-251.
- SCOTT, J. S.
1969. Trematode populations in the Atlantic argentine, *Argentina silus*, and their use as biological indicators. J. Fish. Res. Board Can. 26:879-891.
- SELF, J. T., L. E. PETERS, AND C. E. DAVIS.
1963. The egg, miracidium, and adult of *Nematobothrium texomensis* (Trematoda : Digenea). J. Parasitol. 49:731-736.

SHARP, G. D.

1978. Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. In G. D. Sharp and A. E. Dizon (editors), *The physiological ecology of tunas*, p. 397-449. Acad. Press, N.Y.

SINDERMAN, C. J.

1961. Parasite tags for marine fish. *J. Wildl. Manage.* 25: 41-47.

UCHIYAMA, J. H., AND P. STRUHSACKER.

1981. Age and growth of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, as indicated by daily growth increments of sagittae. *Fish. Bull., U.S.* 79:151-162.

WANKOWSKI, J. W. J.

1981. Estimated growth of surface-schooling skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, from the Papua New Guinea region. *Fish. Bull., U.S.* 79: 517-532.

WATERTON, J. L.

1973. Incidence of *Hirudinella marina* Garcin, 1730 (Trematoda: Hirudinellidae) in tunas from the Atlantic Ocean. *J. Parasitol.* 59:207-208.

YAMAGUTI, S.

1970. Digenetic trematodes of Hawaiian fishes. Keigaku Publ. Co., Tokyo, 436 p.